A NEW SPECIES OF DIRCA (THYMELAEACEAE) FROM THE SIERRA OF NORTHEASTERN MEXICO

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ABSTRACT

A newly discovered population of *Dirca* from the Sierra Madre Oriental of Tamaulipas, Mexico, is described and illustrated here as *D. mexicana* sp. nov. It expands the genus to three species and it is first of the genus known to occur in Mexico. The new species is similar to *D. palustris* of the eastern United States in its long calyx tube with abruptly flaring limb, but its greatest overall similarity is with the rare and restricted *D. occidentalis* of the San Francisco Bay region in west-central California. *Dirca mexicana* resembles the latter in its bud scales with whitish pubescence, sessile flowers and fruits, distinctly lobed calyces, and persistent pubescence on the young twigs and abaxial leaf surfaces. The new species differs from *D. occidentalis* in its flowers with a longer, narrower tube, shorter limb and lobes, and shorter style and filaments; the two population systems are separated by more than 2500 kilometers. *Dirca mexicana* is separated from the closest population of *D. palustris* by more than 1100 kilometers.

KEY WORDS: Dirca, Thymelaeaceae, Mexico

RESUMEN

Una población de *Dirca* recientemente descubierta en la Sierra Madre Oriental de Tamaulipas, México, se describe e iconografía aquí como *D. mexicana* sp. nov. Con ello se eleva a tres el número de especies en el género, siendo ésta la primera que se conoce en México. La nueva especie se parece a *D. palustris*, del este de los Estados Unidos, por su largo tuba del caliz con limbo abruptamente acampanado, pero su mayor parecido general es con la rara y restringida *D. occidentalis* de la región de la Bahía de San Francisco en la región centro-oeste de California. *Dirca mexicana* se parece a esta última en las escamas de las yemas con pubescencia blanquecina, flores y frutos sésiles, cálices netamente lobulados y la pubescencia persistente en las ramas jóvenes y en el envés de las hojas. La nueva especie difiere de *D. occidentalis* por sus flores con un tubo más largo y más estrecho, con limbo y lóbulos más cortos, y estilo y filamentos más cortos. Los dos sistemas de poblaciones están separados por más de 2500 kilómetros. *Dirca mexicana* está alejada más de 1100 kilómetros de la población de *D. palustris* más próxima.

The genus *Dirca* L. has previously included only two species, *D. palustris* L., scattered but widespread in the eastern United States and adjacent Canada, and *D. occidentalis* A. Gray, endemic to six counties of the San Francisco Bay region in west-central California (McMinn & Forderhase 1935; Vogelman 1953; Nevling 1962; various floristic manuals; Fig. 1). On a

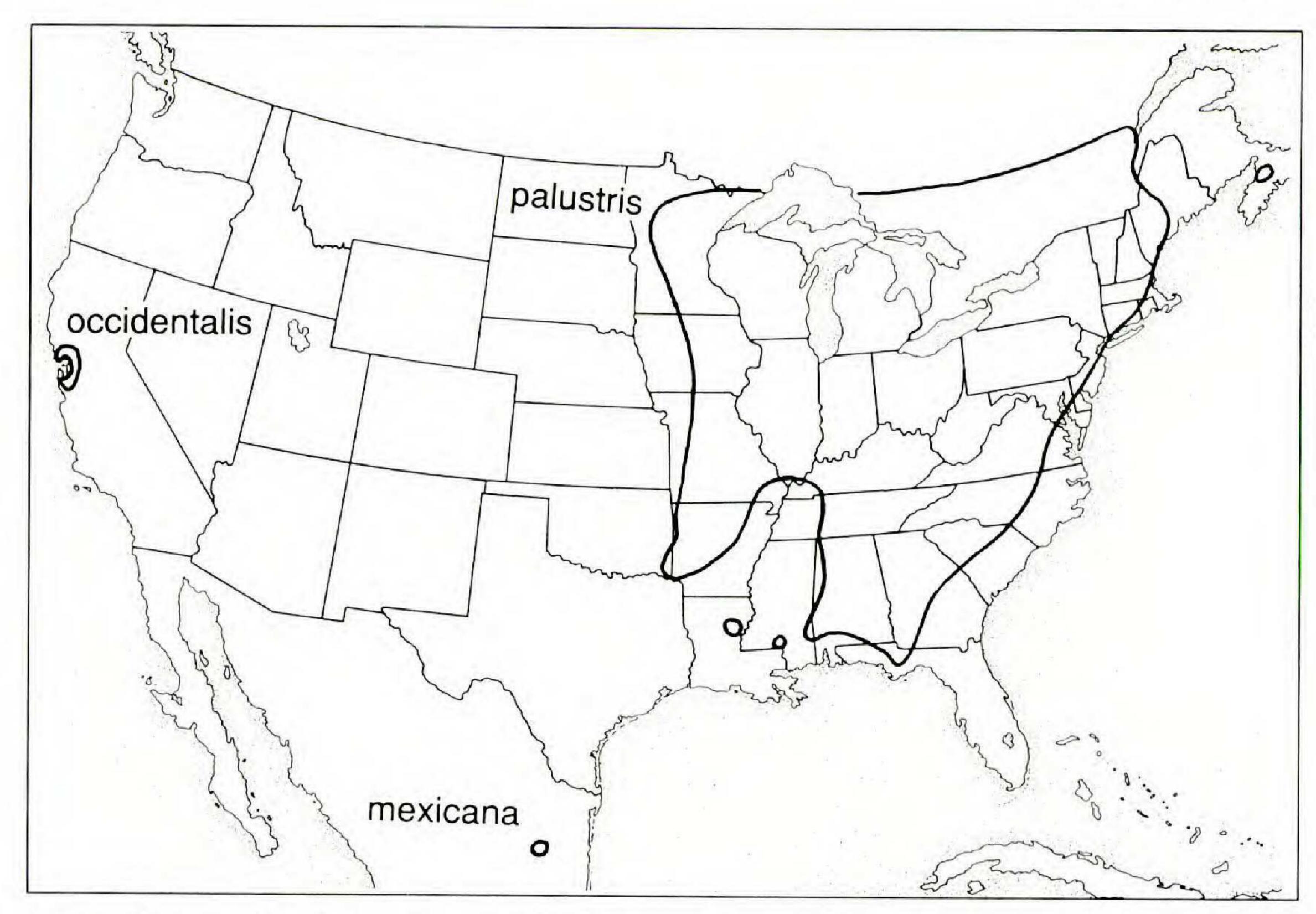


Fig. 1. Geographic distribution of the three species of Dirca.

botanical reconnaissance in September 1994 in the Sierra Madre Oriental of Tamaulipas, Mexico, we observed a population of low shrubs that we recognized as *Dirca*, but the plants were sterile and not identifiable to species. In early March 1995 we were able to study the population at peak flowering and beginning of fruit. The Mexican plants most closely resemble *D. occidentalis*, but there are several consistent morphological differences between them and they are geographically disjunct by more than 2500 kilometers (California/Tamaulipas, see Fig. 1). The closest known populations of *Dirca palustris*, at the southwestern corner of its range in eastern Louisiana, Arkansas, and southeastern Oklahoma, are more than 1100 kilometers disjunct from the Mexican plants. We believe that it is justifiable and desirable to recognize this Mexican population as a species distinct from both of its more northern relatives.

Dirca mexicana Nesom & Mayfield, sp. nov. (Fig. 2)

Differt a Dircae occidentali A. Gray calycibus tubo longiore angustiore limbo breviore, filamentis supra medium calycis insertis, et stylis ac filamentis brevioribus.

Woody shrubs 6–20 dm tall, averaging ca. 16 dm, from a single trunk branched near the base, with spreading, flexuous branches, the stems 2–3(–5) cm wide near the base of the plant, the ultimate branches 2–3 mm wide, bark smooth and grayish to reddish-brown, the current year's growth

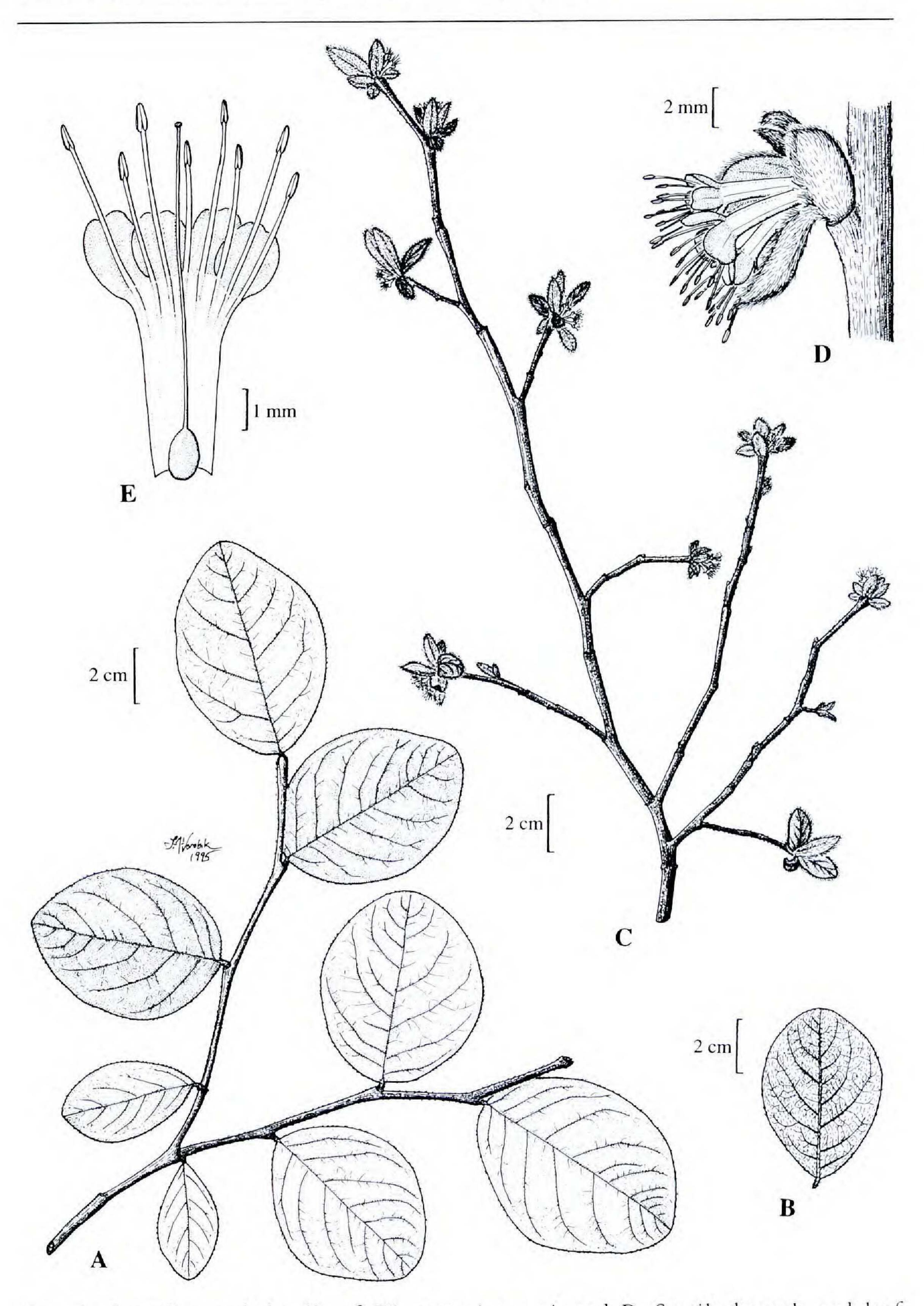


Fig. 2. Branches and details of *Dirca mexicana*. A and B. Sterile branch and leaf (*Mayfield 2085*). C-E. Flowering branch, flower cluster, and single flower, opened (*Nesom 7863*).

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persistently loosely and sparsely pubescent, glabrous below. Leaves deciduous, alternate, entire, at maturity broadly elliptic to slightly ovate, basally rounded, 4–8 cm long, 2.5–6.0 mm wide, 1.3–1.7 times longer than wide, the largest distally situated on the branchlets, glabrous above, the lower surface persistently sparsely strigose-sericeous on the lamina and along the veins, petioles 1–2 mm long. Buds covered by the enlarged petiole base, mixed (flowers and leaves), the apical apparently falsely terminal, the 4 bud scales whitish-sericeous, forming a foliaceous, deciduous involucre to the flowers. Flowers appearing before or concurrently with the leaves, sessile in axillary and apical fascicles, deflexed to somewhat more nodding at full anthesis, the axillary fascicles invariably producing 3 flowers, the apical fascicles sometimes apparently "twinned" with (5-)6 flowers; corolla absent, not represented by infracalycular structures; calyx (7-)8-10 mm long, petaloid, the tube narrow but slightly widening distally, 5-7 mm long, abruptly expanded into a flaring limb 2-4 mm long, the tube/limb ratio (of length) (1.5–)1.7–3.0, the 4 calyx lobes 1.5–3.0 mm long, the lobes and limb yellow, the tube lighter yellow and drying creamy; stamens 8, filaments inserted within the calyx tube essentially at a single level (at the throat, 2.0–3.5 mm below the lobe apex), the longest exserted 2–3 mm above the calyx lobes, those inserted below the lobes 1-2 mm longer than those inserted below the sinuses, the thecae 0.4-0.8 mm long, basifixed; "hypogynous disc" or "disc" (sensu Heinig 1951) a ring of connate, irregular, slightly fleshy scales ca. 0.2-0.4 mm high and wide, basally adnate to the inner surface of the calyx base; stigma minutely capitate, above the level of the pre-dehiscent anthers on a fully elongated style, equalled or slightly surpassed by the dehiscing anthers. Fruits drupaceous, 1-seeded, pyriform to ovoid, sessile, green when young, mature fruits not observed.

Type: MEXICO. Tamaulipas. Municipio. Hidalgo: along mountainous road from Sta. Engracia (Tamaulipas) to Dulces Nombres (Nuevo Leon), Arroyo Obscuro, 2.0 road mi NE of Los Caballos toward Canada El Mimbre, 15.0 road mi W of lowermost crossing of arroyo El Mimbre, 23°59'09"N, 99°28'37"W, ca. 1800 m, 3 Mar 1995, *Guy Nesom* 7863 with Mark Mayfield and Greg Anderson (HOLOTYPE: MEXU; ISOTYPES: AAU, ANSM, ARIZ, ASU, BH, BRIT, CAS, CHAP, COLO, CONN, DAV, DUKE, ENCB, F, FSU, FTG, GA, GH, GUADA, IEB, K, KANU, LSU, M, MICH, MO, MSC, NCU, NLU, NY, OBI, OKL, OS, OSC, P, RM, RSA, S, TENN, TEX, UARK, UAT, UC, UCR, UNL, US, VDB, WIS, WTU, XAL.

Additional collection examined: MEXICO. Tamaulipas: type locality, [sterile, leaves only], 23 Sep 1994, Mayfield 2085 with Nesom (TEX).

Description of the locality.—The site at which Dirca mexicana was observed and collected (Arroyo Obscuro) is a steeply sloping, north-facing, mesic cove surrounding a rocky watercourse. The area is limestone with karstic tendencies. The elevation near the road is ca. 1800 meters, but plants of

Dirca extend to at least ca. 20 meters (elevation) above the road and to at least 80 meters below it. They may well occur over a broader area than we investigated, particularly downslope, but this is the only locality where Dirca was encountered along the 35 kilometer road from Sta. Engracia to Dulces Nombres. Indeed, we found no other site along this road with a similar physical and floristic definition.

The dominant canopy trees at the site are Carya ovata (P. Miller) K. Koch, Pinus patula Schlecht. & Cham., Pseudotsuga menziesii (Mirb.) Franco, and Quercus laurina H. & B. Large trees of these reach about 20-25 meters in height, with tall Pseudotsuga perhaps reaching 30 meters. Judging from stumps in the area, particularly large individuals (presumably of Pseudotsuga and Pinus) have been removed by logging. Large trees of Carpinus caroliniana Walt. and Liquidambar styraciflua L. are scattered at the locality but do not reach the full height of the canopy. The woody understory includes the following: Cornus urbiniana Rose, Croton virletianus Muell.-Arg., Garrya macrophylla Benth., Ilex aff. rubra S. Wats., Litsea pringlei Bartlett, Persea pododaenia Blake, Philadelphus calcicolus Hu, and Taxus globosa Schlecht. Most of the canopy species are deciduous and were just beginning to break bud at this site; the understory includes a predominance of evergreen species. Arboreal bromeliads, including three species of Tillandsia, are conspicuous. Ferns form a major part of the herbaceous flora at this site; among the most common are species of Adiantum, Woodwardia, Botrychium, Phanerophlebia, Polypodium, and Polystichum. Other common herbs include species of Chimaphila, Chiropetalum, Goodyera, Sisyrinchium, and Stachys.

Characteristics of the population and biological observations.—We observed 800–1000 plants (by estimate) at the Dirca site, where they occur for about 300 meters along the road and adjacent slopes on the east side of the water-course. They tend to be densely clustered in more open-canopy microsites, occurring most abundantly toward bottom of cove, but the plants occur singly and more scattered over a larger area. We did not unearth any plants, but there was no indication that they reproduce clonally. A report of rhizome production in D. occidentalis (McMinn & Forderhase 1935) has not been corroborated by more recent observations (Spongberg pers. comm.).

The entire population of *Dirca mexicana* is strongly synchronous in flowering. Had we arrived 3 or 4 days later, it is likely that we would have been unable to observe floral features, as the flowers appear to wither quickly with the onset of fruit maturation. The flowers appear to be weakly protogynous and there is evidence that they also may be self-compatible. Initially, before full development of the calyx, the style (with apical stigma) usually is elongated past the level of the anthers. At this time, the stigma appears slightly moist and presumably receptive; we also observed that

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many at this stage appear to have pollen attached. At full anthesis, the filaments have raised the open anthers to the level of the stigma or slightly beyond it. Further, there is little time separating intial receptivity of the stigma and dehiscence of the anthers, and little distance between the stigma and open anthers.

Visiting the flowers were one species of bee (individuals ca. 7 mm in length) and at least four species of butterflies. Pollination is effective, judging from the apparently ubiquitous deposition of pollen on the stigmata of pre-staminate flowers. Bees and butterflies were probing inside the flowers, and although it seems highly likely that nectar was available to them (probably produced by the hypogynous disc), its production was not evident in numerous flowers that we examined. Nor could we detect any fragrance (*D. occidentalis* was noted by Howell [1970] to be fragrant). Fruit maturation was beginning only on a few plants and we were unable to make an estimate of the success of fruit and seed production.

We did not determine what feature or features account for the remarkable rarity of *Dirca mexicana*. All of the other species yet identified from Arroyo Obscuro are found in other sites in the same general area—none except the *Dirca* could be considered rare (but see comments below regarding *Viburnum*). Rarity, however, also is a feature of both other species of the genus, particularly *D. occidentalis* (Stebbins 1942; Johnson 1994). *Dirca palustris* is widespread but of uncommon occurrence.

Morphological comparisons.—Direa mexicana resembles D. occidentalis in most of the features that have been used to distinguish the latter from D. palustris (Vogelmann 1953; see key below): vestiture, presence or absence of a peduncle and pedicel, and the distal morphology of the calyx. The flowers of D. mexicana, however, are more similar in general configuration to those of D. palustris: both have a relatively long and narrow tube with a shorter, abruptly widening limb, the staminal filaments are inserted above the middle of the calyx, and the style and anthers are exserted for a relatively short length. In D. occidentalis, the tube is shorter than the broadly funnelform limb, the staminal filaments are inserted below the middle of the calyx, and the style and stamens are long-exserted. Vogelman (1953, p. 80) emphasized the taxonomic usefulness of the level of filament insertion, which in turn is indicative of the throat position and flower shape: "In most instances this character alone is sufficient to distinguish the two species." The comparative illustrations furnished by Vogelmann, however, do not accurately represent this difference, nor does the detailed illustration of D. palustris in Cronquist (1981, p. 635); those by Holm (1921) are more similar to our own observations. Differences between the new species and D. occidentalis are summarized in the following key.

1. Bud scales with brown or reddish-brown pubescence; young twigs and both leaf surfaces completely glabrous; flowers and fruits pedicellate, the whole cluster often pedunculate; calyx margin merely crenulate-undulate, with-1. Bud scales with whitish pubescence; young twigs and abaxial leaf surfaces persistently pubescent; flowers and fruits sessile; calyx distinctly and deeply 2. Calyx tube 2-4 mm long, broadened into a broadly funnelform limb 4-6 mm long; staminal filaments inserted below the middle of the calyx, anthers exserted 3-4(-5) mm above the flower at maturity; style and stigma (1-)2-4 mm above the anthers at maturity; San Francisco Bay 2. Calyx tube 5-7 mm long, abruptly broadened into a flaring limb 2-4 mm long; staminal filaments inserted above the middle of the calyx, anthers exserted 2-3 mm above the flower at maturity; style and stigma about level with the anthers at maturity; sierra of northeastern Mexico

Biogeographic pattern.—It does not seem possible at this point to provide a morphologically based hypothesis of relationship among the three species of Dirca, because the genus appears to be relatively isolated, its closest relatives (and thus the evolutionary polarity of character states) difficult to specify (see Domke 1934; Nevling 1959). Still, it is surprising to find a greater overall similarity between D. mexicana and D. occidentalis, in view of the well-known pattern of close relationship and disjunction between species of the eastern and southeastern United States and the sierra of northeastern Mexico (Miranda & Sharp 1950; Graham 1973). In the immediate area of Dirca mexicana are numerous species that are disjunct from their primary range in the eastern United States (e.g.): Carpinus caroliniana, Carya ovata, Chimaphila umbellata (L.) W. Barton, Desmodium glutinosum (Muhl. ex Willd.) Wood, Liquidambar styraciflua, Pedicularis canadensis L., and Polystichum acrostichoides (Michx.) Schott. In addition, there is a rare and yet undescribed species of Viburnum (Nesom in prep.) in the close vicinity that apparently is most closely related to V. obovatum Walt. of the southeastern United States. Another recently recognized, disjunct species from the same area of Tamaulipas, Scrophularia sp. nov. (Mayfield and Nesom submitted), is closely similar to S. marilandica L. of the eastern U.S. species and S. californica Cham. & Schlect. of the Pacific region. Taxus globosa, one of the understory species at the Dirca site, also has close relatives widely separated in the eastern and western United States.

Biotic disjunctions between the eastern and western United States, similar to that in *Dirca*, are well known though not particularly common (e.g., Sharp 1951; Wood 1970), and other examples can easily be added (e.g., *Sericocarpus*, *Ionactis*). This pattern is emphasized by the recent discovery of

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a second species of *Neviusia* in California (Shevock et al. 1992), both species extremely rare. In contrast, clearly established disjunctions of extant plants from the western United States to the Sierra Madre Oriental of Mexico are unknown to us. Numerous disjunctions exist between the Sierra Madre Oriental and S.M. Occidental, but most or all of these appear to be derivatives of the general pattern described by McVaugh (1952), where the evolutionary antecedents occupy a more southern position. A few Mexican species have a broken but still somewhat continuous distribution from the eastern sierra through northern Coahuila into the mountains of southwestern Texas and southeastern New Mexico (e.g., *Populus tremuloides* Michx., *Pseudotsuga menziesii* [Mirb.] Franco, and see Nesom 1993).

In the broadest view of the origin of Dirca mexicana, the simplest hypothesis is that it belongs to the floristic element with its closest evolutionary ties to the flora remaining in the southeastern United States, the geographic continuity between them probably established during the middle to late Miocene (Graham 1973). The disjunction between D. palustris and D. occidentalis may be considerably older, as a vegetation probably including these species was spread across North America through much of the Tertiary, beginning as early as the Eocene (Graham 1972, 1993). In a contrasting view, Axelrod (1975) hypothesized that the closely related disjuncts found in eastern Mexico, the Appalachians, and the West coast of the United States represent remnants of a continuous forest earlier spread into Mexico and more simultaneously fragmented as a result of a spreading dry climate in the mid-Oligocene. Evaluation of the latter theory is difficult at present because of the lack of evidence for northern temperate elements in Latin American prior to the Late Tertiary. These elements have not been recovered from the Oligo-Miocene Simojovel Group of Chiapas, Mexico; Quercus first appears in Panama in the Mio-Pliocene, and in South America Alnus arrives by about one million years ago and Quercus not until about 340,000 years ago. Many eastern North America disjuncts were present in eastern Mexico by the middle Pliocene, and global paleotemperature history suggests that cooling in the middle Miocene may have been an appropriate time for their principal introduction.

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